OBSERVATIONS ON THE ECOLOGY AND NATURAL HISTORY OF ANURA IX. NOTES ON BREEDING BEHAVIOR IN OKLAHOMA[1]

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It is well known that some single species of frogs or toads may breed at different times of year and use somewhat different types of breeding sites in different portons of their geographical ranges. This seems to be especially true of those forms whose distribution is of wide extent, particularly if the range traverse several degrees of latitude (Wright and Wright, 1933). It is less commonly understood that the details of breeding or other habits may vary, usually slightly but sometimes markedly, in different ecological situations; and that such changes of habits are often of great importance in the adjustment of a given species to the differences in various habitats within its geographical range (Bragg, 1940d; see also Blair, 1941). Because of these facts, it is not safe to generalize concerning the breeding habits of any species of Anura from its study in one locality only. Instead, one must study these habits in each ecological community wherein the species is found to determine (1) whether any variations in breeding pattern occur, and (2) if so, what factors (ecological or physiological) are involved in the changes. Only in this way can we approach complete understanding of the adjustment of a species to its environment and of the reasons for its geographical distribution and possible ecological segregation.

The breeding habits of Anura in Oklahoma are still imperfectly known. Those of some species of Bufo have been analyzed and notes on some others have been given in the earlier papers in this series (Bragg, 1940, 1940a, b, c, d, 1941; Bragg and Smith, 1942). The habits of *Scaphiopus bombifrons* Cope were given consideration by Trowbridge and Trowbridge (1937). Except for these papers, only incidental notes have been found in the literature dealing specifically with the Oklahoma forms as observed within this state. Since we have made observations upon breeding habits, breeding dates, and breeding sites in connection with our extensive field trips in Oklahoma during the past four years, it seems desirable that our findings be presented.

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Our general method of procedure has been to follow the weather reports as given by the local press or radio and to take trips at night during spring, summer, and autumn from Norman to other parts of the state wherever and whenever heavy or violent rains were reported. Since most species are influenced in their breeding behavior by the coming of rain, this method has enabled us to locate hundreds of breeding congresses and to observe the breeding reactions in as much detail as individual circumstances made to seem desirable. Our observations have naturally been more intensive, as well as more extensive, within a fifty-mile radius of our starting point at Norman in central Oklahoma. They have been least extensive in the panhandle. We have, however, visited at least once every one of the seventy-seven counties in the state.

Twenty-five species or subspecies of Anura are recognized as occurring in some part of Oklahoma. Of these, seven of the rarer forms have not been observed by us in breeding congresses. Three others have been found only a few times. The remaining fifteen have been seen often enough to justify our belief that we understand, at least in broad outline and often in some detail, the breeding pattern exemplified by each in Oklahoma. This is especially true as to the characteristic breeding sites used and as to the extent of the breeding season.

The observations are presented in three divisions: (1) the earliest and latest breeding date observed, together with other pertinent data, are presented for each species in Table 1; (2) annotated lists of breeding sites are given; and (3) miscellaneous unpublished observations on the breeding behavior of several species, thought for one reason or another to be of special interest, are presented. Identificacations of all forms are by us. Specimens have been deposited in the University of Oklahoma Museum of Zoology.

In the preparation of Table 1, care has been taken to report only those congresses of Anura which we have reason to believe were of such nature that eggs were eventually produced. Slight rains often stimulate a few males of some species to start calling without this resulting in actual breeding. Often, calling hylas and sometimes even calling ranas and bufos do not indicate breeding. The finding of tadpoles in pools we have taken, of course, as proof that breeding has occurred but these have been used as indicative of a breeding date only in exceptional circumstances: for example, if tadpoles of *Scaphiopus bombifrons* or *Bufo cognatus* are found two weeks after the only rain has occurred in the region, one seems justified in fixing the

date of egg production as on the night following the rain or within two or three days thereafter.[2] This is because these species breed only after rain. A similar situation involving any species of Rana, *Bufo w. woodhousii,* or *B. a. americanus* in Oklahoma does not necessarily indicate this. In all such cases, we have used our best judgment based upon our total experience. It should also be noted that in construction of Table 1, the number of congresses reported is not the actual number visited in the course of this study. On some of our trips we have found areas as large as whole counties which sounded like one huge chorus of amphibian voices. We may have visited as many as fifteen or more separate congresses in such an area on a single night. Ordinarily we have considered such cases as one experience for each species represented at each type of breeding site within the area and have so recorded them in Table 1.

Weather data given in this paper are from three sources: (1) from summaries obtained from the U. S. Weather Bureau at Oklahoma City, (2) from the local station at the University of Oklahoma, and (3) from our own observations of air and water temperatures taken in the field in a few instances.

BREEDING SITES

Breeding sites for Anura in Oklahoma are quite varied in character. In the wooded and hilly regions of eastern Oklahoma, streams are often clear and, in some reaches, fairly swift. Some, however, like the Kiamichi, are in some parts sluggish, deep, and muddy. In the region of the mixed-grass prairie (central Oklahoma) most streams are trancient, their floodplains being either broad sandy wastes or deep dry ravines for long periods between floods. Small streams entering such rivers as the Canadian or Cimarron in central Oklahoma, especially from the east or north, are often blocked by sand dunes and form sloughs along the edges of the flood-plain. Such sloughs vary much in character with the season, with the amount of rainfall, and with local conditions. They may be muddy or clear and, during the hot weather of summer usually run through the cycle typical of stagnant water anywhere, eventually disappearing altogether if not replenished by rains. Several species of frogs and toads utilize these sloughs for breeding, especially in early spring.

Muddy cattle tanks are present in large numbers in almost all

(2) *B. cognatus* may call for from one to five nights under the stimulation of a single rain; *S. bombifrons* may call from one to three nights. Eggs of the former are most often laid on the second night, those of the latter, on the first.

regions of Oklahoma. Buffalo-wallows occur in all of the mixed-grass and most of the short-grass prairies, i. e., from the central portion of the state westward. They do not occur in the more sandy soils of the eastern part of the state nor in the sand prairies of the short-grass association in the west. They cannot occupy these regions because the sandy soil fails to become puddled to such extent as to hold the water. Buffalo wallows may have either clear or muddy water, depending upon local conditions. In the mixed-grass prairie, they are more commonly clear, unless located in severely overgrazed pastures.

Flooded fields and ditches are of several different kinds. In some regions, such areas may be very extensive and, although temporary, quite deep after heavy rains. We have waded waist-deep in temporary water on several occasions. On the other hand, some extensively flooded fields are shallow, not more than one foot at the deepest part, and often with an acre or more of water only a few inches in depth. Either type may be muddy or clear depending upon local conditions; but shallow, temporary water, whether in fields or ditches, is more often clear than muddy. In contrast, deep temporary water in Oklahoma is usually muddy.

As will be seen from the following lists, some species use only certain types of these sites for their breeding activities; others use several. This ecological segregation is best noted when radically different conditions are found in two pools situated close together. On several occasions in central and western Oklahoma we have found *Bufo cognatus* separated in this way from *B. woodhousii woodhousii* (see also Bragg, 1940 and 1940a). In one case we found them segregated in two parts of the same pool. The local situation was a peculiar one. A fence separating two fields crossed a depression in which the pool was formed. One field had been plowed; the other had not. During a violent shower, muddy water from the plowed field rushed into the depression from one side while clear water drained from the grass-covered unplowed field opposite. The result was a pool in which the water graded from quite clear at one end to excessively muddy at the other. The whole pool was shallow and only slightly deeper on the muddy side. There was a large chorus of *B. cognatus* at and near the clear end of the pool and a smaller number of *B. w. woodhousii* (probably about twenty) calling in the muddy section. We found no evidence of the mixing of the two species.

Some species are kept apart within a single breeding site by the reactions of individuals of both sexes to the calls of their own species

(see Bragg, 1940a for a case of this kind among several species of Bufo). Other closely related species do not intermingle much due to different reactions of the males. This is well seen in Scaphiopus. *S. couchii* often breeds in the same pools with *S. bombifrons* in southern and southwestern Oklahoma. Males of the former call from the bank or from very shallow water at the pool's edge. Females gather about a male in a sort of semicircle. Eventually, the male jumps and catches a female and they enter the water together (Ortenburger, 1924). Males of *S. bombifrons* seldom call from the bank (we have observed this on two occasions). Usually they call sprawled out on the water and attract their females to them here (Trowbridge and Trowbridge, 1937). In this way these two species are segregated until females have been mated. There is some indication that other species of Scaphiopus may be segregated in the same manner. This is suggested by our limited observations on *S. hurterii* and also by those of Smith and Leonard (1934) who found this form breeding with *S. bombifrons* in central Oklahoma. It is not quite clear how this segregation works when *S. bombifrons* occupies the same pool as *S. hammondii* but some recent observations in New Mexico suggest strongly that there is such a mechanism (Bragg, 1941a). We have not seen these species together in Oklahoma.

Some closely related species are known to be interfertile and others are strongly suspected of being so. Such differences in habits as described above will go far toward explaining why interbreeding is so infrequent in nature even though two interfertile species may use the same water at the same time. (See also Blair, 1940, 1941). When such factors are not operative for any reason, as when a species changes its habits at the border of a range, interbreeding may occur more frequently. The detailed study of habits, therefore, may be of great value to those interested in intergradation of subspecies where ranges meet.

OUTLINE OF BREEDING SITES AND THE SPECIES USING THEM IN OKLAHOMA

1. *Permanent deep water* (rivers, artificial lakes, deep ponds). *Acris crepitans* and *Rana sphenocephala* on or near the edge in shallow water, usually among aquatic vegetation. *Rana catesbeiana* calling on or near the bank, eggs floating in deeper water. *Bufo w. woodhousii* commonly breeds in muddy backwashes of large rivers and creeks and occasionally in artificial lakes of whatever size. *B. w. fowleri* was found calling in numbers on the muddy bank of the slow-flowing and

deep Kiamichi river one night. Tadpoles of the same species have been found in clear deep water of the Mountain Fork River in McCurtain County.

2. *Small, clear-water streams* (eastern and southern Oklahoma). *Bufo americanus americanus* and rarely *B. w. woodhousii* in shallow flowing water; these species and *Acris crepitans, Hyla versicolor versicolor, Pseudacris triseriata,* and *Rana sphenocephala* in shallow backwashes and overflow areas. *B. w. fowleri* also used clear, sandy-bottomed streams.

3. *Sloughs and backwashes on the floodplains of muddy creeks and rivers* (certainly of the Arkansas, Cimarron, Canadian, and N. Canadian and probably of the Red) *Bufo a. americanus* occasionally (two observations), *B. w. woodhousii* very abundantly, *Rana sphenocephala* very abundantly, *Pseudacris triseriata* rarely and in small numbers.

4. *Sloughs of relatively clear water on the floodplains of large rivers. Acris crepitans* and *B. w. woodhousii* very abundantly; *Pseudacris streckeri* characteristically; *Rana sphenocephala* very commonly; *Ps. triseriata* (one observation).

5. *Flooded shallow fields and shallow ditches of clear water, usually with considerable vegetation protruding through them. Bufo cognatus, B. compactilis, Microhyla olivacea, Pseudacris clarkii, Ps. triseriata, Scaphiopus couchii,* all in large numbers; *B. w. woodhousii, Ps. streckeri, Rana sphenocephala,* and *Scaphiopus bombifrons* in small numbers. *Bufo insidior* has been taken in this situation in small numbers also but the small numbers are thought to be due to the comparative rarity of this species.

6. *Buffalo wallows of clear water or similar small shallow clear-water pools. Bufo cognatus, B. compactilis, Microhyla olivacea, Ps. clarkii,* and *Ps. triseriata,* often in large numbers; *Scaphiopus bombifrons* in small numbers.

7. *Deep, muddy pools of all sorts* (ditches, flooded fields, cattle tanks, etc.). *Bufo americanus, B. woodhousii fowleri, B. w. woodhousii, B. compactilis, B. insidior,* (in shallow water near edge); *Hyla versicolor versicolor, Rana areolata areolata, Rana sphenocephala, Scaphiopus couchii, S. hurterii,* and *S. bombifrons* (characteristic breeding site). *Rana catesbeiana* is often present in large numbers in some such pools and has been heard calling in them once or twice. They breed here sometimes, for their tadpoles have been found in cattle-tanks.

8. *Rock-bottom pools of small extent. Bufo punctatus* embryos,

just hatching, were found once in the Wichita Mountains (Bragg and Smith, 1942).

9. *Pools in creeks. Acris crepitans* and *Rana sphenocephala* occasionally.

The condition as to roiliness and depth of water may be summarized thus:

1. *Species characteristically breeding only in clear, shallow, temporary pools. Bufo cognatus,* and *Ps. triseriata.*

2. *Species to which roiliness of the water seems to make little difference. Acris crepitans, Bufo a. americanus, B. compactilis, B. w. woodhousii, Hyla v. versicolor, Microhyla olivacea, Pseudacris streckeri, Ps. clarkii, Rana spenocephala, Scaphiopus bombifrons, S. couchii, S. hurterii.*

3. *Species usually using water not more than 10 inches (usually less) in depth. Acris crepitans,* all species of Bufo, *Hyla v. versicolor, Microhyla olivacea,* all species of Pseudacris with the exception of *Ps. streckeri,* probably *Rana a. areolata* (too few observations for certainty).

4. *Species usually requiring deep water (one foot or more). Rana catesbeiana, R. sphenocephala* (some exceptions), *Scaphiopus bombifrons, S. couchii,* and *S. hurterii. S. bombifrons* sometimes breeds in shallow water in small numbers (buffalo wallows). In New Mexico it sometimes uses very shallow pools (Bragg, 1941a), and we have on two occasions found males in shallow water in Oklahoma.

MISCELLANEOUS OBSERVATIONS

A. *The Breeding Season*

The question of a breeding season among several species is of some interest. Most species of frogs and toads are thought to have a quite definite breeding season, in the southern states often more extensive than in the northern. Except for the fact that most Oklahome species breed only in the warmer months (March to September), we find that several forms have no such season; and those which do not have one are typically those species especially adapted to life in the prairie (Bragg, 1940d, 1941: Bragg and Smith, 1942). Other species have a definite breeding season here, as well as elsewhere. Three species are of special interest in this respect, *Pseudacris streckeri* Wright and Wright, *Microhyla olivacea* (Hallowell), and *Scaphiopus bombifrons* Cope.

Ps. streckeri breeds (or at least calls vigorously) in midwinter in

Oklahoma. The earliest record is that of January 1 (1941) following heavy rains. On this date thousands of males were calling in Pontotoc, Coal, and western Hughes counties during a day somewhat warmer than usual for this season.[3] At Norman, they have been heard in numbers in the sloughs of the Canadian river many times between February 1 and mid-May. Rain after May 23 does not seem to stimulate further breeding activities. The earliest that we have known a female to produce eggs was on the night of February 26, but these eggs did not develop. It would seem, therefore, that *Ps. streckeri*, like its close southern relative, *Ps. ornata* (Holbrook) tends to have an exceptionally early breeding season. We have records of males calling at an air temperature of 0 degrees C. and in water near 0° C. (For details of breeding habits, see Bragg, 1942.)

Microhyla olivacea is in marked contrast to the above. We have heard this species only incidentally before April 30 and usually not in numbers before May 8. From this time on through the summer into September, it breeds only after rains; and any rain of appreciable amount will bring them to pools and ditches in numbers. We have often found clasped pairs and eggs in pools containing well-developed tadpoles, and in several other instances, have observed metamorphosing young leaving a pool in which males were calling vigorously and females were present. This is a species, therefore, which starts its breeding rather late in the spring, at least in Oklahoma, thereafter following the rains throughout the summer. It seems probable that earlier breeding is inhibited by low temperatures.

Scaphiopus bombifrons is especially interesting, since our observations indicate interpretations somewhat different from those of some other workers. It is often stated or implied that the plains spadefoot typically emerges to breed only once in a season in any one locality. We find this not to be true, either in New Mexico (Bragg, 1941a) or in central Oklahoma. Three large congresses developed at Norman, Oklahoma in the spring and early summer of 1940, coming on May 21-22, June 12-13, and July 2-3, in each case during or immediately after very violent or heavy rains. There were also several large congresses here in the spring of 1941.

Trowbridge and Trowbridge (1937) studied this species over a period of three years at Norman. Among other things, they point out that for the period from 1934 to 1936 inclusive, this spadefoot did

(3) We are indebted to Mr. O'Rielly Sandoz, while acting as ecological field worker for the Oklahoma Fish and Game Commission, for these observations.

not breed after the first spring rain but did breed later in the spring of each year after rains, sometimes of less extent than those which had come earlier. They found also that the spadefoots did not breed until at least a total of 3.66 inches of precipitation had accumulated. From this evidence they thought it probable that *S. bombifrons* has a definite breeding season, modified by the coming of rain and that a certain amount of precipitation must accumulate before breeding activity commences. It was clearly stated that this conclusion was only tentative and an appeal was made for other workers, who had opportunity, to check it.

This we have attempted to do from observations made principally in the area studied by the Trowbridges at Norman and often from experiences at the same pools visted by them. It is deemed best to present the evidence in some detail in order that our observations may be compared with theirs. The observations cover the five-year period from 1937 to 1941 inclusive. During 1937 one of us (Bragg) was in the field with A. H. Trowbridge and in 1938 and 1939 with M. S. Trowbridge to whom we are indebted for certain observations and notes. All remaining observations were made by us and the interpretations of all of the observations were made without consultations with the Trowbridges. We are, therefore, wholly responsible for the conclusions drawn.

In 1937, Febraury was very dry at Norman, only 0.31 inches of precipitation being recorded. In March, the total was 2.17 inches, the largest amount (0.55 in.) falling on the 13th. April had a total of 1.83 in., most of it coming in a single storm on the 20th. (1.25 in.). The total precipitation from February 1 to April 20 inclusive was 4.11 inches, i. e., 0.34 in. above the minimum found effective as a breeding stimulus by the Trowbridges. The spadefoots did not breed at this time, despite the fact that the minimum temperature on the day of the storm was not below that critical for emergence (see beyond). The rainfall in May totaled 2.13 inches. The spadefoots did not breed after rains of 0.57 in. on the 11th, or 0.96 in. on the 30th, amounts which at other times have brought them out in this and other areas. Temperatures were much too high to have had an inhibiting influence. June continued rather dry and the weather became hot. Light showers of from 0.10 to 0.48 in. fell during five of the first ten days. On the 16th a sharp shower brought 0.66 in. of rain and that night A. H. Trowbridge and one of us found a small congress south of the university campus. Several clutches of eggs were produced here and, later, tadpoles were found in a buffalo wallow nearby which had been

dry before the storm. There had been a total of 8.54 inches of precipitation since February 1, most of it in the form of light showers or slow rains.

In 1938, a total of 7.35 inches of precipitation fell in February, all storms of 0.90 inch or more at temperatures low enough to inhibit breeding, even if it could otherwise have occurred. March was dry till the 26th, a total of only 0.35 in. in two showers being recorded. On the 26th a storm totaling 2.02 in. came. That night, the temperature was 9° C. and no breeding occurred. The following day had intermittent showers totaling 0.90 in. That evening spadefoots were calling in numbers all about Norman at a temperature at just less than 12° C. The following day was rainy (total 2.19 in.). There had been a total precipitation of 5.11 inches in three days. That night, the whole country-side was reverberating with anuran calls, the spadefoots in great numbers among them. The temperature at 9:15 was just less than 12° C. and at 1:00 A. M. it had risen to 14° C. Numerous clutches of eggs were produced in at least a dozen breeding sites about Norman. There was no further breeding activity either in April or after rains in May which brought out *B. cognatus*. Observations were not made in June or July.

In 1939, precipitation in March totaled 1.86, most of it in one rain (1.03 in.) on the 28th and 29th. Temperatures were too low (3° C. at one time) for breeding. April was dry (total 0.51 in.) but May had 4.18 in., the largest storm being 1.27 in. on the 13th. The species did not breed. June had numerous light showers with a rain of 1.6 in. on the 12th. and another of 0.95 in. on the 25th. The first congress of spadefoots occurred on June 28th during and after a rain totaling 3.78 in. The total for June prior to this time was 3.84 in.

The season of 1940, in some respects, showed more than those of the previous three years. Total precipitation for the spring months was as follows: February, 3.18 in.; March, none; April, 4.25; May (to the 21st), 3.39. Significant storms occurred as follows: Apr. 5-6, 1.33 in.; Apr. 11, 1.30 in.; Apr. 28, 1.20 in.; May 16, 0.65 in.; and May 21-22, 1.80 in. The spadefoots first emerged to breed on the night of May 21 after a particularly violent storm late in the afternoon. As mentioned earlier, there were also two other heavy congresses at Norman late in the spring and early in the summer.

These observations may be summarized as follows: (1) *Scaphiopus bombifrons* bred only after rain in each of the four years. (2) The least rain after which they bred was 0.66 in. (June, 1937). (3) The least accumulated rain before their breeding was 6.44 (1937). (4)

They sometimes did not breed after more than an inch of rain when the accumulated precipitation was more than the minimum observed by the Trowbridges. (5) They usually did not breed after the first spring rains and often failed to do so after rains greater in amount than other rains after which they had been observed to breed at other times. (6) *S. bombifrons* failed to breed below a temperature of 9° C., but did breed abundantly at just below 12° C. when other conditions seemed favorable (observations of 1938). We may set the temperature below which they do not ordinarily breed as close to 11° C.

From the above facts, it is evident that at least one factor not shown in the observations of the Trowbridges must be operative as a stimulus for the initiation of breeding behavior. Further analysis of the data indicates that this is the violence of individual storms. One-half inch of rain falling within one-half hour is often as great a stimulus as more than twice this amount spread out through a period of several hours. Both the absolute amount of rain and its rate of fall are factors in the situation, the largest congresses developing during and after heavy rains in which sharp showers fall, i. e., when both factors are operating together. Below are presented some observations which tend to illustrate these things.

The rain of April 20, 1937, totaling 1.25 in., was slow and progressed through several hours. Notes, written on that date, say, "It rained intermittently nearly all day. *B. cognatus* were calling in numbers tonight but only a single *S. bombifrons* was heard." Contrast this with the notes taken on June 17, 1937. "Estimated about one-half inch of rain in the hour before nine A. M. Later, hot most of the day, out in the evening in bright moonlight south of the campus. Congress of Scaphiopus in cornfield, attaching eggs to leaves of Polygonon sp.—water temperature at the surface, 38° C., six to eight inches below, 29° C." Another illustration came on May 12, 1939. A rain totaling 1.27 inches fell slowly during most of the night. No spadefoots were found out the night of the 13th; but on June 28 they bred abundantly after what the notes say was a "heavy rain in several showers" (total, 3.78 inches). A third experience is of special interest because it illustrates to some extent the intensity of the stimulus of a very violent storm. This occurred near Clinton in western Oklahoma. On April 11, 1940, the Norman Transcript carried a story of a violent storm in this region. Among other things it said, "A hail storm slashed at Clinton and nearby Arapaho for thirty minutes last night—automobiles were swept into ditches as water gushed from a

2.44 inch downpour." The U. S. Weather Bureau corroborates the newspaper's statement as to the amount of precipitation but indicates that "The hail storm continued for about one hour." The storm was accompanied by a marked drop in temperature, the lowest reading of the month at Clinton (24° F.) being recorded on the 12th. This is much below the critical temperature for the emergence of *S. bombifrons* as found at Norman. On the night of the 13th, we visited this area. A medium sized congress of *S. bombifrons* was found in a deep cattletank about three miles northeast of Clinton in water uncomfortably cold to wade. Both males and gravid females were present. Hailstones were still piled along one side of the tank. No other Anura were found breeding between Arapaho to the north of Clinton and the northern city limits of Cordell, Washita County, to the south. Since the temperature was much too low immediately after the storm, it is probable that no spadefoots bred before the night of the 13th. That they did so on the 13th indicates that the exceptional violence of the storm constituted a stimulus so great that the breeding urge remained through two days of cold weather becoming expressed in a breeding congress as soon as the slowly rising temperature allowed.

The above experiences are only samples of several similar observations in various parts of Oklahoma. See also Bragg (1941a) for observations in New Mexico. Our total experience, therefore, indicates the following conclusions as regards the initiation of breeding behavior of *S. bombifrons*: (1) Breeding may occur at least between late March and early July in Oklahoma whenever the following conditions are met: (a) the temperature must not be lower than about 11° C., (b) it must have rained at least about 0.50 in., (c) a small amount of rain falling as a violent shower is a greater stimulus than a much larger amount coming slowly over a longer period of time. (2) There is no true breeding season in this species; breeding can occur at any time in spring or summer when the conditions outlined above obtain.[4] (3) The amount of accumulated moisture in the springtime as emphasized as a possible factor by the Trowbridges has

(4) August breeding in Oklahoma is still unobserved. However, it has been seen in the plains of Kansas (H. M. Smith, 1934), which is something like Oklahoma ecologically, as well as in New Mexico (Bragg, 1941a). It seams probable that the scarcity of records in summer in Oklahoma is due in part to the very hot dry weather characteristic of July and August in most years and in part to the fact that during most seasons storms of the violent type come in spring so that most spadefoots have a chance to complete their breeding before summer. It does not seem probable that they would repair to breeding pools after rain if their sex products have already been shed. The gonadal cycle undoubtedly has some influence.

either negligible or no effect upon the breeding of this species. (4) The fact that the spadefoots do not always breed after the first spring rains is due to the effect of low temperatures, to the lack of violence of the individual storms, or to the combined effect of these two factors.

B. *Time of Day During which Breeding Occurs*

The time of day during which anuran breeding occurs in Oklahoma varies somewhat with conditions and with species. As might be expected, most breeding congresses are built up at night; when they occur in the daytime, they usually foretell a much larger congress in the evening and through the night of the same day. Such species in central Oklahoma, where most detailed observations have been made, include *Bufo cognatus, Pseudacris clarkii* and *Microhyla olivacea.* More rarely *Bufo w. woodhousii* and *Scaphiopus bombifrons* behave in this manner also. Another group of species may start calling, often in large numbers, at any time of day or night. In central Oklahoma *Acris crepitans, Pseudacris triseriata,*[5] and *Ps. streckeri* are examples. Concerning the second of these, we have several times heard congresses in bright sunshine about Norman only to find the pool completely silent when we returned in the evening to secure specimens.

Daylight breeding congresses are true breeding aggregations. We have often found clasping pairs within them, especially of the bufos.

C. *Effect of Severe Cold on a Breeding Congress of Bufo w. woodhousii*

Below about 13° C., *B. w. woodhousii* rarely starts breeding activity; but if a large and active congress is in progress when the temperature falls suddenly to freezing or below, this continues to the probable production of eggs. Observations supporting these statements follow.

After a 1.33 in. rain on April 6 and 7, 1940, a very large mixed chorus of *B. w. woodhousii* and *Pseudacris streckeri* developed on the evening of the 10th. in the sloughs of the Canadian river near Norman. Many clasping pairs of the bufos were observed in water four to six inches deep at about 9:30 P. M. At about midnight, a heavy thundershower accompanied by a violent north wind brought cold weather

(5) This is the species of Pseudacris mentioned by Bragg (1940a) as unrecognized in Cleveland County.

(min. temp. 5° C.) and a continued wind (20 miles per hour near the ground) the next day. A visit to the breeding site early in the afternoon revealed that conditions were much as the day before, except that there was much more water in the sloughs. Males were still calling in small numbers, mated pairs were present (about twenty were counted) mostly lying on the bottom or along the edge where the latter were buffeted by waves. No eggs could be found and none of the pairs were producing them. Evidently conditions were such that females refused to lay their eggs even though many had been clasped for a long time by males. Some of the toads were slow and lethargic, particularly the mated pairs on the bottom. Others were still alert to danger and some of the unmated males plunged into the water when approached. The temperature continued to fall and the next morning was below freezing (26° F.) although it had warmed to 40° F. by noon. Another visit to the breeding site at 2:00 P. M. showed conditions to be almost exactly as the day before.

Because of making trips to other parts of the state, observations were discontinued here until the 25th, on which date thousands of tadpoles of *Bufo w. woodhousii* were present. They appeared to be about two weeks old, judging by their size. Since they could not have come from eggs laid before the 10th, and probably not before the 13th, we think it likely that they came from the mated pairs seen here during the cold wave. Assuming this to have been the case and interpreting on the basis of our hypothesis as to the function of the clasp of the male (Bragg, 1941), the cold inhibited the functioning of the pituitary until the weather warmed on the 13th and 14th. Then normal breeding was resumed.

D. *Position of the Males of Some Species While Calling.*

Rana areolata areolata often calls while sprawled out on the water something after the manner of the plains spadefoot. While thus engaged, it is not particularly disturbed by a flashlight and is relatively easy to collect. Some individuals of this species, as well as of *R. sphenocephala*, call from the bank. *Pseudacris clarkii*, like most other members of this genus in Oklahoma, usually utters its breeding call from under banks or from clumps of vegetation to which it is hanging with its hands. Sometimes, however, it calls in umbers from tall grasses some distance from the water. This usually occurs in late afternoon prior to a night very favorable for the breeding of this species and almost always after rains. This probably occurs as the

males are moving in towards the pools to form a breeding congress, for the whole appearance is as though the little fellows just cannot wait to find water before starting their calls. The habit may have a function such as the guilding of other members of the species to proper pools but of this we are not certain.

Scaphiopus hurterii has been seen by us in breeding congresses on a few nights only. Males in one congress called from temporary muddy pools bordering a flooded ditch in water about three feet deep. These were spread out on the water. Others in this congress called from shallow water near the bank. Some miles away, another congress had developed in a shallow muddy ditch. Some were sitting in the muddy water and others were calling from the bank, completely out of water. In 1941 they bred three times in one pool under observation but did not enter a slightly deeper pool near by. These observations suggest those of Smith and Leonard (1934) on a congress of this form in Cleveland County, Oklahoma. We are able to confirm also that the call of this form is distinctive. It is a single not unpleasing squawk given rather suddenly and explosively at intervals of about two seconds. It has some carrying power but is not nearly so loud as that of *S. bombifrons*. Judging from the work of Ball (1936), our observations on the call and calling position tend to confirm the anatomical evidence of H. M. Smith (1937) that *S. hurterii* is distinct, taxonomically, from *S. holbrookii holbrookii* (Harlan).

E. *The Call of Bufo w. woodhousii*

Attention was given earlier to the fact that *B. w. woodhousii* has two radically different types of call (Bragg, 1940a). We have since found that the typical breeding cry of this subspecies is surprisingly variable in character. It is sometimes a very short call; at other times much longer. Often it is hoarse; at other times, much higher. The various variations are next to impossible to describe but they are quite evident in almost any fairly large congress in any part of the state. One variation, given several times consistently by two different individuals in different breeding congresses, suggests the cry of a young human baby. The variations do not seem to be correlated with size of individuals, type of breeding site, or the numbers present.

SUMMARY

Intensive and extensive field observations over several years on the breeding of Anura in all parts of Oklahoma form the basis for an

analysis of breeding sites, breeding dates, and a series of miscellaneous notes on isolating mechanisms tending to show ecological segregation even of closely related forms. The principal conclusions are: (1) Some species in Oklahoma have a breeding season in the usual sense of this term—others do not. (2) In the latter, initiation of breeding behavior is brought about by the coming of rain. (3) The prairie-limited species invariably breed only after rain; those not so limited may be stimulated by rain but commonly breed without it. (4) Breeding sites differ for different species: Some prefer clear water, some muddy water, others show no selection on this basis; some use only shallows, others only deeper lakes, rivers or ponds; some use only temporary water, others only permanent water, and still others both. (5) Interspecific isolation in breeding within one pool is often effected partly or solely by differential behavior of males, of females, or both, particularly in regard to the attention paid to the call of the male and in the specific behavior pattern of the males in securing mates.

A considerable discussion of observations over a period of four consecutive years shows that the tentative conclusions of Trowbridge and Trowbridge (1937), namely that *Scaphiopus bombifrons* breeds only after a certain amount of precipitation has accumulated, is unfounded. Instead, this animal breeds at any time, at least from late March to early September, after *violent* (as opposed to *heavy*) rains provided the temperature is not below approximately 9° C. Most breeding occurs after heavy rains coming in several violent showers, but a violent rain of as little as 0.5 in. is a greater stimulus than one of 2.0 inches which falls slowly.

A table of inclusive breeding dates observed for nineteen of the twenty-five species known in Oklahoma is presented.

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TABLE 1

Dates between which breeding has been observed for several species in Oklahoma. A summary of breeding sites in included.

Organism	Times seen breeding				Dates (min.-max. records)		Breeding sites
	Call only	Pairs seen	Eggs or larvae	Total breeding record			
Acris crepitans	65	3	10	78	4/2	8/17	shallow pools, stream margins
Bufo a. americanus	42	17	15	74	4/3	6/28	streams, ditches, ponds, tanks
B. cognatus	126	50	40	216	3/3	8/9	shallow clear pools, ditches
B. compactilis	8	3	0	11	4/16	8/9	shallow pools, ditches
B. insidior	3	2	0	5	4/29	8/9	shallow pools
B. punctutus	0	0	1	1	5/7	5/7	very small rock pools
B. w. fowleri	15	0	3	18	6/10	6/16	river margins, small lakes
B. w. woodhousii	120	45	40	205	4/4	8/9	any standing shallow water
Hyla v. versicolor	30	15	10	55	4/15	8/24	tanks, flooded creeks, ditches
Microhyla olivacea	102	26	20	148	4/16	9/4	shallow temporary water
Pseudacris clarkii	105	9	7	121	3/31	9/4	grassy clear pools, ditches
Ps. triseriata	21	1	2	24	3/30	6/23	grassy clear pools, ditches
Ps. streckeri	65	3	10	78	1/1	5/23	clear sloughs, ditches, fields
Rana a. arcolata	3	0	0	3	4/13	4/13	ditches, fields
R. catesbeiana	6	0	17	23	4/16	6/7	lakes, large streams
R. sphenocephala	72	40	97	209	2/12	9/4	all standing water except buffalo wallows
Scaphiopus bombifrons	45	22	20	87	3/27	7/3	deep temporary pools
S. couchii	8	1	1	10	4/16	8/9	tanks, fields
S. hurterii	4	0	4	8	4/15	9/4	ditches, gravel pits, ponds
Total	840	237	295	1372			

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